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PRELIMINARY INVESTIGATIONS INTO THE AGE AND GROWTH OF THE SHORTFIN MAKO, *ISURUS OXYRINCHUS*, WHITE SHARK, *CARCHARODON CARCHARIAS*, AND THRESHER SHARK, *ALOPIAS VULPINUS*, IN THE WESTERN NORTH ATLANTIC OCEAN

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SUMMARY

Preliminary analysis of the vertebrae of these three species indicate that the current processing method is adequate for counting bands. Sample collection is ongoing and it is likely that more will be obtained for the shortfin mako and thresher shark, though not for the white shark. Complete studies on the age of these species using the entire vertebral samples, tag/recapture data and length frequency analysis for verification are ongoing. Validation of band pair periodicity, which is critical for obtaining accurate ages, will be included in these studies. Information resulting from these studies will include species and sex specific growth rates, size at age, age at maturity, and longevity. The results of this preliminary analysis indicate that the vertebral centra are appropriate structures to use for aging these species. Because of the exploratory nature of these analyses and inadequate samples sizes these data should not be used to estimate growth function parameters for analytic results.

RÉSUMÉ

L'analyse préliminaire des vertèbres de ces trois espèces indique que la méthode actuelle de traitement est adéquate pour le comptage des anneaux. La collecte d'échantillons est en cours, et il est probable que plus d'échantillons soient obtenus pour le requin-taupe bleu et le requin-renard, mais pas pour le grand requin blanc. Des études complètes sur l'âge de ces espèces d'après des échantillons de vertèbre entière, les données de marquage/recapture et l'analyse des fréquences de taille pour la vérification sont en cours. Ces études comprendront la validation de la périodicité des paires d'anneaux, qui est critique pour obtenir l'âge précis. L'information issue de ces études comprendra le taux de croissance de l'espèce et spécifique du sexe, la taille à l'âge, l'âge de maturité et la longévité. Les résultats de cette analyse préliminaire montrent que les vertèbres constituent une structure appropriée pour la détermination de l'âge de ces espèces. Vu le caractère expérimental de ces analyses et la taille inadéquate des échantillons, ces données ne devraient pas servir à estimer des paramètres de la fonction croissance en vue de résultats analytiques.

RESUMEN

El análisis preliminar de las vértebras de estas tres especies indica que el método actual de procesamiento resulta adecuado para el recuento de bandas. Continúa la recopilación de muestras y es probable que se obtengan más muestras de marrajo dientuso y zorro, aunque no de tiburón blanco. Se están realizando estudios completos sobre la edad de estas especies utilizando muestras de vértebras enteras, datos de marcado y recaptura y análisis de frecuencias de talla para fines de verificación. En este estudio se incluirá la validación de la periodicidad de los pares de bandas, la cual resulta crítica para la correcta determinación de edades. La información proveniente de estos estudios incluirá tasas de crecimiento específicas por sexos y por especies, tallas por clase de edad, edad de maduración y longevidad. Los resultados de estos análisis preliminares indican que los centros de las vértebras son estructuras apropiadas para determinar la edad de estas especies. Dado al carácter experimental de estos análisis y las inadecuadas tallas de las muestras, estos datos no deben

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utilizarse para estimar los parámetros de la función de crecimiento para obtener resultados analíticos.

KEYWORDS

Age determination, Growth curves, Life history, Longevity, Shark fisheries

1. INTRODUCTION

The shortfin mako, *Isurus oxyrinchus*, is distributed throughout the temperate and tropical regions of the world's oceans. Detailed migratory studies on the shortfin mako in the western North Atlantic show that members of this species prefer a temperature range of 17-22^{o}C (Casey and Kohler 1992). Makos move north from Cape Hatteras as the inshore waters warm beginning in April and May moving into southern New Jersey waters by early June and the New York waters by mid to late June. By August they are found in Maine and Nova Scotian waters (Casey and Kohler 1992). Though not targeted commercially in U.S. waters, makos are caught as by-catch and as well as being subjected to an intensive recreational fishery, primarily off the New England states, New York and New Jersey (Casey and Kohler 1992). Age estimates were obtained for the shortfin mako in the western North Atlantic by Pratt and Casey (1983). They could not validate their age interpretations, however, and concluded that band pairs were deposited biannually (two band pairs deposited per year). The biannual theory of band periodicity in lamnoids has been under continued debate. Parker and Stott (1965) first suggested biannual band pair deposition in their study of the basking shark, *Cetorhinus maximus*. Pratt and Casey (1983) followed this with their study on the shortfin mako (Pratt and Casey 1983) and Branstetter and Musick (1994) suggested biannual band pair deposition for the sand tiger shark, *Carcharias taurus*, based on marginal increment analysis (MIA). However, studies on mako sharks from other oceans and current lamnoid age research does not support the contention of biannual band pair deposition (Wintner and Cliff 1999, Natanson et al. in press). Cailliet et al. (1983, 1985) assumed annual band pair deposition for Pacific coast shortfin mako and white sharks. Wintner and Cliff (1999) stated that they could not determine band periodicity using MIA in the white shark off the coast of South Africa, though one tetracycline injected (OTC) recapture suggested annual deposition. More recently, Natanson et al. (in press) validated annual band pair deposition in the porbeagle, *Lamna nasus*, with known age individuals and direct OTC methods up to an age of 11 years. With the exception of Natanson et al. (in press) and Winter and Cliff (1999), direct validation of band periodicity, such as OTC injection or known age tag/recaptures, has not previously been reported in lamnoids. In view of these two recent studies, which contradict the biannual band pair deposition hypothesis, a revision of the age estimates for the shortfin mako using updated techniques and increased sample sizes with an emphasis on obtaining validation is being undertaken.

The white shark, *Carcharodon carcharias*, occurs in coastal and offshore waters and is most common in cold and warm temperate seas (Compagno 1984). In the western North Atlantic, it is found from Newfoundland to the Gulf of Mexico (Casey and Pratt, 1985). White shark sightings are common off New England during the summer (Casey and Pratt, 1985). Prior to being listed as a prohibited species in 1998 in US waters (NMFS 1999), white sharks were sought after by recreational fishermen. It was not unusual for them to be weighed in at sportfishing tournaments or for large specimens to be landed on Long Island, NY, during August. White sharks have been aged from the eastern Pacific using vertebrae without validation (Cailliet et al. 1985). Wintner and Cliff (1999) aged white sharks in South Africa using vertebrae with marginal increment analysis and one OTC recapture for validation. To date, no age study has been conducted on white sharks from the North Atlantic.

The thresher shark, *Alopias vulpinus*, is a pelagic species with a nearly circumglobal distribution in warm waters (Compagno 1984). It is found throughout the western North Atlantic Ocean from Newfoundland to Cuba and into the Gulf of Mexico (Compagno 1984). Little is known about the thresher's migratory patterns, however, data collected at shark fishing tournaments along the northeastern U.S. coast from New Jersey to Massachusetts, show that this species is in the region by mid-June. They move north into the waters off Massachusetts and Maine by July where they remain. These sharks can be found in this region until October (NMFS unpub. data[2]). All size ranges of males and females including pregnant and recently post-partum females are seen in June (NMFS unpub. Data[2]). Young of the year threshers are found off the coast of North Carolina in the fall, indicating the possible presence of a nursery area (C. Jensen pers. comm.[3]). The thresher shark is not targeted by a commercial fishery but is taken as incidental catch and as a sport fish. Early observations from the Apex Predators Program indicate that thresher sharks may go through long cycles of abundance and decline (Casey et al. 1981). Shark tournament observations prior to 1975 show few, if any, threshers landed. Between the mid- 70s and 80s threshers were sporadically landed. Tournament landings have gradually increased since the mid-1980's and remained fairly consistent, though at a low level, with notable exceptions; for example 1999, a total of 37 threshers were caught at two tournaments held on the same weekend in June; more than is usually reported from tournaments in an entire season (NMFS unpub. Data[2]). Cailliet et al. (1983) generated von Bertalanffy growth parameters for thresher sharks in California waters using vertebrae and length-frequency methods. Welden et al. (1987) attempted to validate the vertebral counts using radiometric dating, but the results were inconclusive. The thresher shark has not been aged in the western North Atlantic.

The Apex Predators Program (APP) of the National Marine Fisheries Service (NMFS) is currently conducting age and growth studies on these three species for the western North Atlantic. Methodology, sample sizes and preliminary findings will be discussed.

2. MATERIALS AND METHODS

2.1 Vertebral Aging

Vertebrae from all species were obtained from sharks caught on commercial and research vessels and at sportfishing tournaments. Sampling took place along the western North Atlantic coast between Prince Edward Island, Canada and the east coast of Florida, U.S.. Multiple vertebrae were removed from the area just above the shark's branchial chamber whenever possible, with the exception of commercially valuable specimens, where samples were obtained closer to the head. On rare occasions, caudal vertebrae were collected and in some cases the entire vertebral column was removed. Vertebrae were then dried, stored frozen, in 70% ETOH or 10% Formalin until processed.

With rare exceptions, only samples that had measured fork length (FL - tip of the snout to the fork in the tail, over the body) or total length (TL - tip of the snout to a point on the horizontal axis intersecting a perpendicular line extending downward from the tip of the upper caudal lobe to form a right angle, over the body; Kohler et al. 1995) were used. All lengths reported in this document are over-the-body FL unless otherwise noted. All conversions used in the study are from Kohler et al. (1995) with the exception of the TL to FL relationship for the thresher shark calculated in this study:

$$FL = 0.5331\,(TL) + 9.5834 \quad n=73 \; r^2 = 0.90$$

In shortfin mako and white sharks, weight was occasionally the only actual measured parameter; in which case, it was converted to FL using the regressions in Kohler et al. (1995).

One vertebra from each sample was removed for processing. The centrum was sectioned using a Ray Tech Gem Saw[4] with two diamond blades separated by a 0.6 mm spacer. Each centrum was cut through the middle along the sagittal plane and the resulting "bow-tie" sections were stored individually in capsules in 70% ETOH. Each section was digitally photographed with a MTI CCD 72 video camera attached to a SZX9 Olympus[4] stereo microscope using reflected light. All samples were

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photographed at a magnification of 4X. Band pairs (consisting of one opaque and one translucent band) were counted and measured from the images using Image Pro 4[4] software. Measurements were made from the midpoint of the isthmus of the full bow-tie to the opaque growth bands at points along the internal edge of the corpus calcareum (Fig. 1a). The radius of each centrum (VR) was measured from the midpoint of the isthmus to the distal margin of the intermedialia along the same diagonal as the band measurements.

The birth band, as indicated by a change in the angle of the centra, is often the most pronounced first band (Fig.1a-c). To confirm the position of the birth band, the size at birth was calculated by multiplying the birth band radius (BR) by the ratio of the vertebral radius (VR) to the FL at capture. The calculated birth size was then compared to known sizes at birth from the literature. Average BR was also compared to VR measurements of young of the year (YOY) sharks. Since this study is preliminary and no validation has been accomplished, subsequent bands were counted using the criteria for the porbeagle, which is a closely related species and has validated annual bands (Natanson et al. in press).

Bands were counted two times by one reader (shortfin mako and white shark) and once each by two readers (thresher shark). Each specimen was read without prior knowledge of either the length or previous count. Initial band counts were compared and specimens were reread if counts did not coincide.

The relationship between VR and FL was calculated in order to confirm the interpretation of the birth band and to determine the relationship between these parameters. Preliminary results indicate that this relationship is linear for the shortfin mako and white sharks (Figs 2,3) a slight curvature is evident at the upper end of the thresher shark relationship, based on two large individuals (Fig.4)

Von Bertalanffy growth functions (VBGF) were fitted to the length at age data by using the following equation (von Bertalanffy 1938):

$$L_t = L_\infty\ (1\text{-}e^{-K(t-to)})$$

where L_t = predicted length at age t;
L_∞ = mean theoretical maximum fork length;

K = a growth rate parameter (yr^{-1}); and
t_o = the theoretical age at zero length.

The VBGF was calculated by using the non-linear regression function in Statgraphics[3].

2.2 Tag/Recapture - Shortfin Mako

Data from the NMFS Cooperative Shark Tagging Program (CSTP) were used for tag/recapture analysis. Sharks were tagged and recaptured by biologists and commercial and recreational fishermen. All measurements were converted to FL by using the morphometric conversions reported in Kohler et al. (1995). Only those sharks reliably measured at both tagging and recapture were used in the analyses. Reliability was based on prior knowledge of the individuals measuring the shark or detailed questioning of those individuals as to the method used. The majority were sharks measured by NMFS biologists or their representatives.

The Gulland and Holt (1959) model was used to generate a growth VBGF from the tag-recapture data. The Gulland and Holt (1959) method uses graphical interpretation of the recapture data to produce estimates of L_∞ and K. Specifically, annualized growth rate (cm/yr) was plotted against average FL (cm) between tagging and recapture to calculate linear regression coefficients. The slope of the line is equal to $-K$ and the x-axis intercept is equal to L_∞.

3. RESULTS AND DISCUSSION

3.1 Shortfin Mako

Vertebral samples from 265 (115 male; 132 female; 18 unknown sex) shortfin mako samples ranging in size from 64 to 340 cm FL have been collected since 1969. Shortfin makos are born at approximately 63 cm FL (70 cm TL) (Castro 1983, Mollet et al. 2000) and grow to 370 cm FL (400 cm TL) (Bigelow and Schroeder 1948). Thus most of the size range is represented by our complete sample size (Fig. 5). A subsample of 19 of these (11 male, 8 female), ranging in size from 94.5 to 328 cm FL were processed for the current analysis.

Calculated size at birth ranged from 52-71 cm FL (mean ± 95% CI birth size = 63 cm FL ± 2.7 cm, n = 19). The close correspondence of the calculated size at birth to reported size at birth indicates that the band was correctly identified.

There was no appreciable difference in the counts between readings one and two. Agreement was achieved on 89% (17) of the vertebrae, 5% (1) disagreed by one band and 5% (1) disagreed by two bands. Agreement was reached on the third count of these two vertebrae.

Preliminary analysis of these vertebrae indicates that the previous ages for the shortfin mako (Pratt and Casey 1983) were underestimated. Pratt and Casey (1983) used four techniques to determine age for the shortfin mako: vertebral counts, juvenile length-frequency data, tag recapture analysis and temporal analysis of length-month information. Based on consistency between methods, they concluded that band periodicity was biannual. These methods were all primarily based on sharks less than 155 cm FL and the subsequent growth does not verify larger sized fish. The band counts from the current study support Pratt and Casey's (1983) original band counts on sharks greater than 150-160 cm FL but disagree with their assigned age estimate (Fig. 6). Conversely, band counts from the current study on sharks less than 150 cm FL disagree with the bands counts from the 1983 study but agree with the assigned age estimate and also correspond to the growth estimates based on Pratt and Casey's (1983) other three methods. Data from the current analysis indicate that Pratt and Casey (1983) may have overestimated the number of band pairs on centra of small sharks. Since this was the portion of the growth curve used as a comparison with the other methods, the decision to divide their counts in half to make the vertebral growth coincide with the other methods may have been unfounded and resulted in vastly overestimating the growth rate in larger fish. The continuation of this study will help to clarify this issue.

The von Bertalanffy growth curve generated from these initial band counts must be viewed cautiously due to the low sample size and lack of validation. The low end of the curve has an unrealistically high size at birth (Fig. 6). It is not unusual that a high size at birth results from the VBGF in shark studies (Cailliet et al. 1983, Wintner and Cliff 1999, Natanson et al. in press) and it may be an artifact of the growth function or low sample size. The analysis of the remaining samples may help explain this finding. The upper portion of the growth curve agrees well with both the new counts and Pratt and Casey's (1983) band counts. Cailliet and Bedford's (1983) growth curve for Pacific Ocean shortfin makos shows slower growth for that population (Fig. 6).

3.1.1. Tag/Recapture

Between 1962 and 2000, members of the CSTP tagged 5,333 and recaptured 608 shortfin makos. A total of 14 were recaptured with sufficient information for tag/recapture analysis. Time at liberty ranged from 0.5 to 2.0 years and size at tagging ranged from 74 to 137 cm FL. Since all sharks tagged were less than 140 cm FL and the largest recapture was 183 cm FL, extrapolations of growth past the latter size cannot be made. Due to the preliminary nature of the analysis, all the data were used in the Gulland model. The growth curve obtained from these data agreed with the band counts for sharks of this size range as well as with the assigned ages from Pratt and Casey (1983) (Fig. 6).

The longest time at liberty for an shortfin mako in the CSTP is 12.8 years. This male mako was tagged at an estimated 183 cm FL and was recaptured at a measured 252 cm FL. The vertebral band count was 17+. Based on the current growth curve the shark would have been 5+ years old at tagging making it 18+ years old at recapture. This is higher than the direct estimate from the growth curve of 12+.

3.2 White Shark

Vertebral samples from 112 (54 male, 51 female, 7 unknown sex) white sharks ranging in size from 112 to 526 cm FL have been collected since 1963. A subsample of 15 (7 male, 7 female, 1 unknown sex) of these ranging in size from 117 to 526 cm FL were processed for the current analysis. White sharks are born between 108 and 136 cm FL (120-150 cm TL; Francis 1996) and are known to reach 599 cm FL (640 cm TL; Castro 1983, Compagno 1984). The total size range is represented in our vertebral sample collection, although most of the samples are from sharks less than 350 cm FL (Fig. 7). Due to the designation of this species as prohibited in the U.S. Shark Fishery Management Plan (NMFS 1999), we are unlikely to add to this sample.

Calculated size at birth ranged from 108.9 to 136.0 cm FL (mean ± 95% CI birth size = 124.7 cm FL ± 7.3 cm, n = 10),. This size range concurs with the known size at birth (Francis 1996). Centra from four free-swimming white sharks ranging in size from 117 to 126 cm FL had no visible bands indicating that the birth band is deposited sometime after birth.

Using the criteria established for the porbeagle (Natanson et al. in press) bands counts were reasonably repeatable. Agreement between the initial two counts was achieved on 53% (8) of the vertebrae, 33% (5) disagreed by one band and 13% (2) disagreed by two bands. Consensus agreement was reached on the third count.

The VBGF generated from the band counts did not fit the data (Fig. 8). Band counts show an increase with size for the first three years as expected. However, three samples that are in the mid-size range appear to have more bands than would be expected. The lack of fit of the VBGF is probably due to the low number of samples at the upper end as well as the presence of these three samples. More samples need to be processed to fill in the growth curve and determine if these three are simply slower growing individuals. Aside from these three individuals, the band counts follow the VBGFs of both of the previous studies on white sharks (Cailliet et al. 1985, Wintner and Cliff 1999) (Fig. 8). Wintner and Cliff (1999) had evidence for validation of annual band periodicity from the vertebrae of one shark that was tagged, injected with tetracycline and recaptured. Validation for the whole size range, however, has not been accomplished. Annual band periodicity was assumed in Cailliet et al. (1985). Due to the prohibited status afforded this species in many locations including but not limited to: Australia, US Atlantic and Gulf Coasts, California and South Africa, it is unlikely that direct validation using tetracycline can be accomplished in these areas.

3.3 Thresher Shark

Vertebral samples from 171 (74 male; 91 female; 6 unknown sex) thresher sharks ranging in size from 62 to 262 cm FL have been collected since 1976. A subsample of 13 (9 male, 4 female) of these ranging in size from 90 to 241 cm FL were processed for the current analysis. Thresher sharks are born at 69-92 cm FL (114-155 cm TL) and are thought to reach 341 cm FL (640 cm TL) (Bigelow and Schroeder 1948, Castro 1983, Compagno 1984) though 274 cm FL (488 cm TL) is a more common maximum length (Castro 1983). The maximum reported size of the thresher shark in the NMFS database is 299 cm FL (533 cm TL; NMFS unpub data[1]). The majority of the size range is represented in our vertebral collection, however, more sharks less than 160 and larger than 250 cm FL would improve the sample (Fig. 9).

Calculated size at birth ranged from 53.5 to 74 cm FL (mean ± 95% CI birth size = 68.3 cm FL ± 4.2 cm, n = 13), this size is slightly smaller than published size at birth indicating that the birth band is formed just prior to birth or that the first band is actually a pre-birth band. Pre-birth bands have been identified in several placental shark species (Casey et al. 1985, Branstetter and Stiles 1987) and are thought to mark the time of placental formation. However, Alopias species are not placental (Liu et al. 1999, Moreno and Moron 1992). Cailliet et al. (1983) did not report on the presence of pre-birth bands in the thresher from the Pacific Ocean.

In general, the second reader undercounted the band readings of the first reader on the larger samples. Agreement was reached on 38% (5) of the vertebrae, 15% (2) disagreed by one band, 31% (4) disagreed by 2 bands and 15% (2) disagreed by three bands. After recalibration between the readers, reader two recounted and consensus agreement was reached.

The preliminary band counts and the associated VBGF show the typical elasmobranch growth pattern (Fig. 10). Both the Cailliet et al. (1983) and the current curves overestimate the size at birth. Cailliet et al. (1983) had fewer bands at size than in the current study. This difference could be due to differences in population growth, preparation technique or the criteria for determining a band pair (Tanaka et al. 1990). Cross reading between laboratories could help determine if it is either of the latter possibilities and validation of the band pair periodicity will determine if the criteria are appropriate. Validation was attempted on this species using radiometric dating (Welden et al 1987) however, the results were too variable to be used. Electron microprobe analysis provided independent verification of the band counts on two specimens and the centrum edge analysis indicated annual band periodicity (Cailliet and Radtke 1987). Direct validation has not yet been accomplished on the thresher shark.

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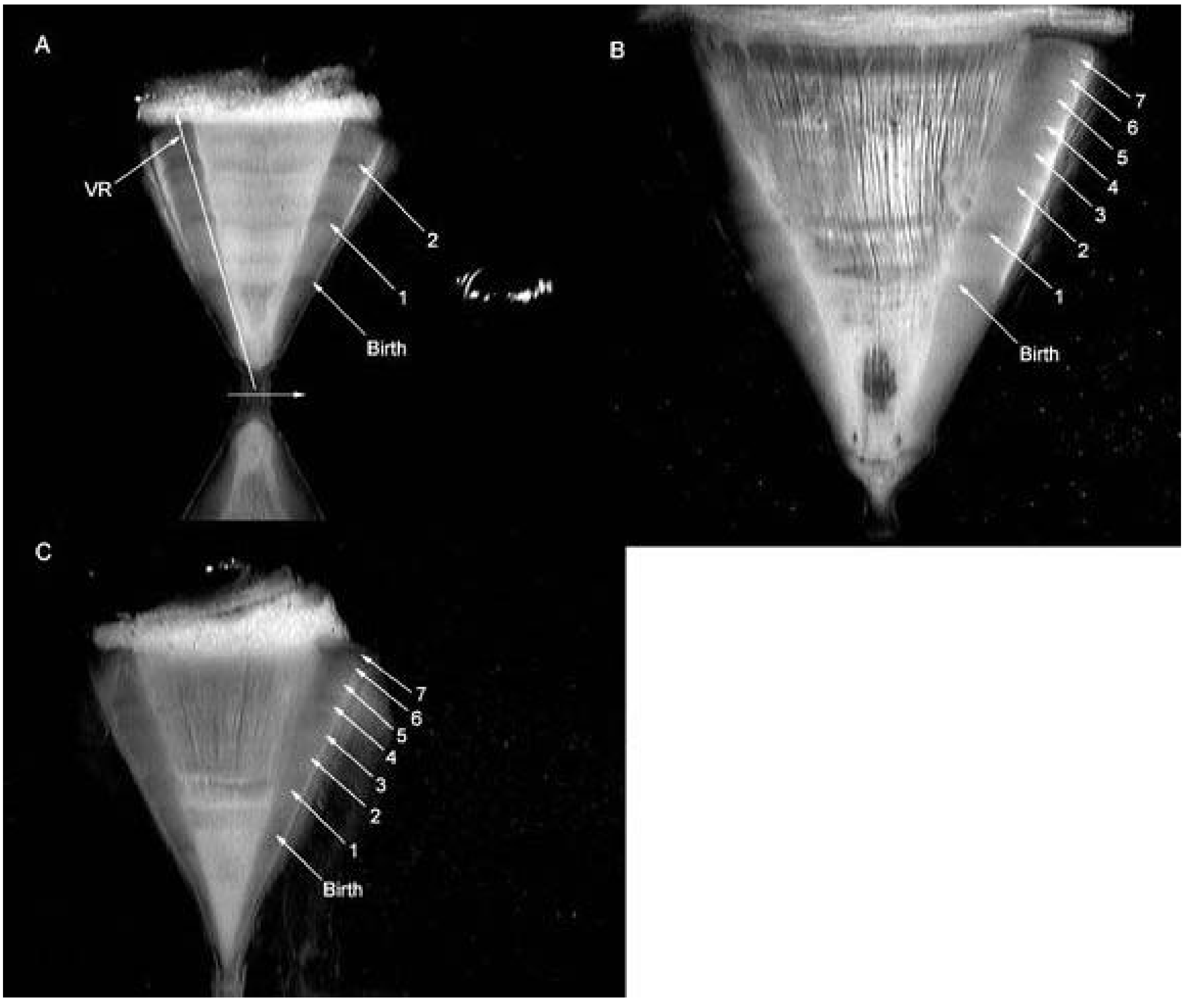

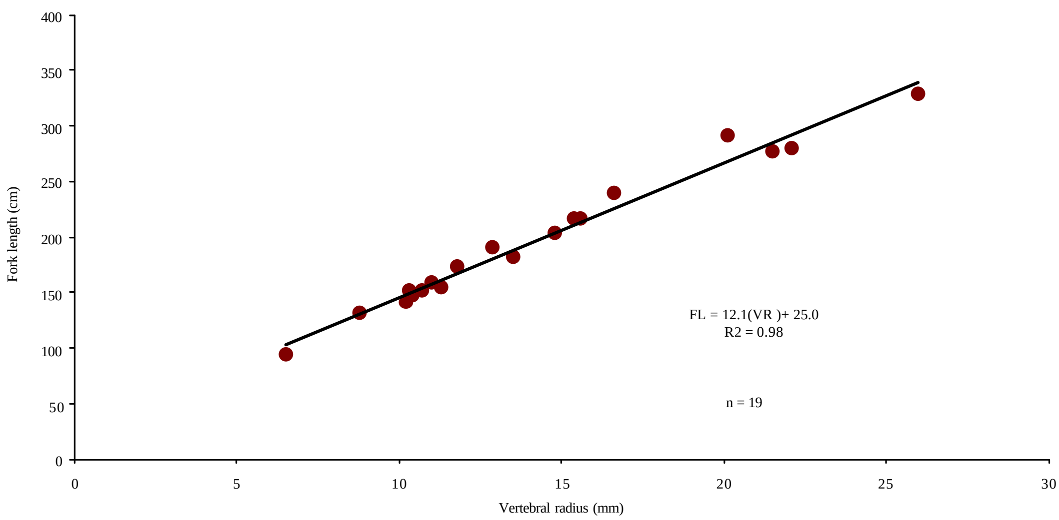

Figure 2. Relationship between vertebral radius and fork length for male and female thresher sharks.

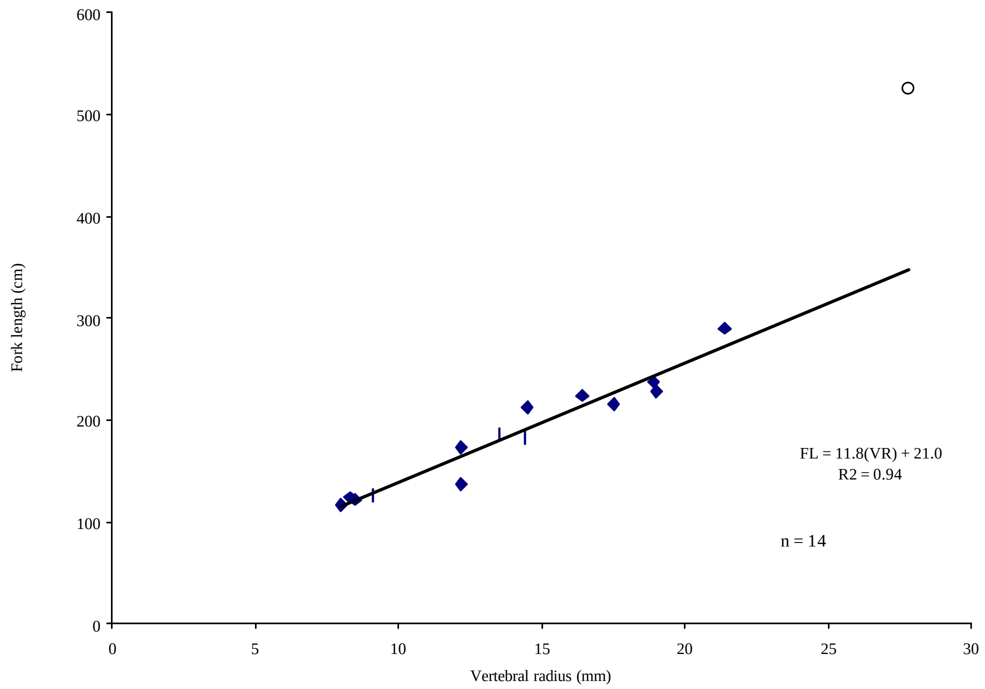

Figure 3. Relationship between vertebral radius and fork length for male and female white sharks. Open circle represents one sample of caudal vertebrae not included in the regression.

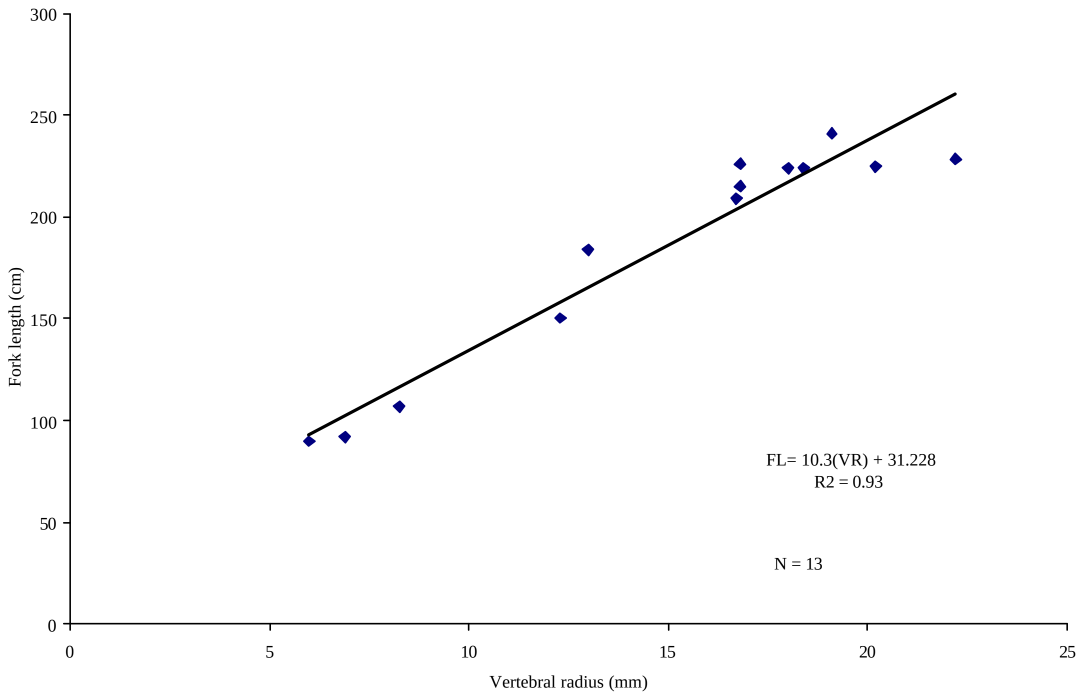

Figure 4. Relationship between vertebral radius and fork length for male and female thresher sharks.

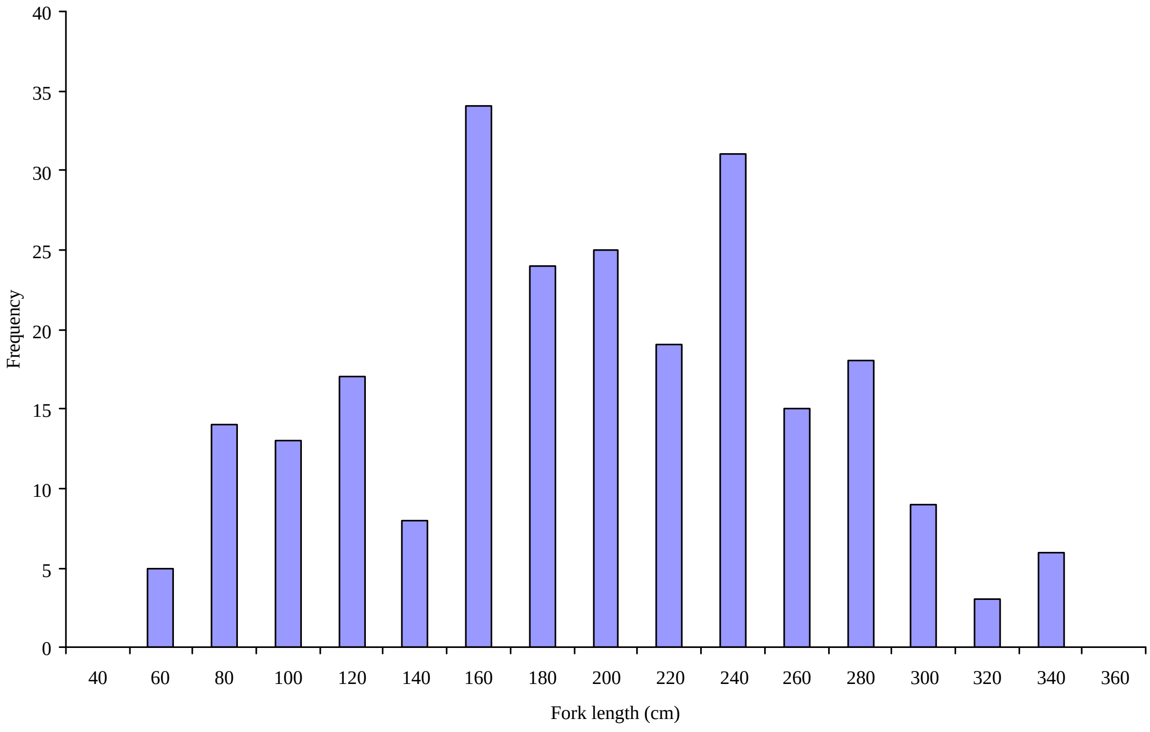

Figure 5. Length frequency histograms of the fork lengths of shortfin makos for which vertebrae are available. n=241.

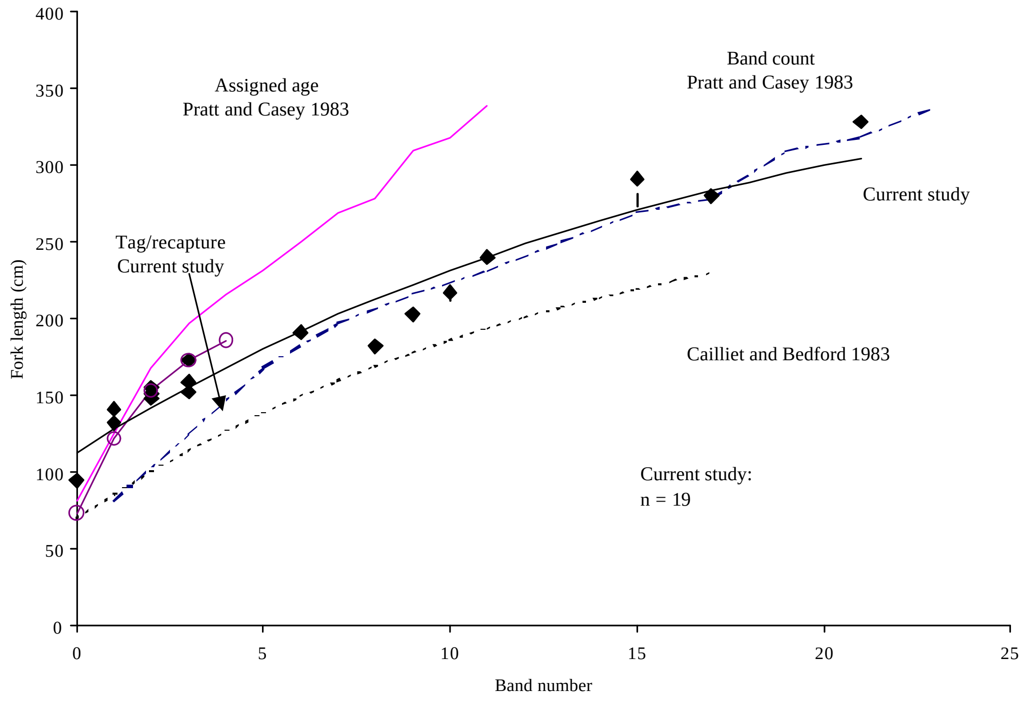

Figure 6. Comparison of shortfin mako growth data. Solid diamonds are the vertebral band counts from this study, thin solid line is the vonBertalanffy growth curve associated with these counts. Open circles with solid line is the von Bertalanffy growth curve from 14 measured tag/recaptures generated in this study. Dashed line represents the von Bertalanffy growth curve generated by Cailliet and Bedford (1983), Dashed line with dots represent the size at band counts data from Pratt and Casey (1983) and the solid line are the age assignments for Pratt and Casey (1983).

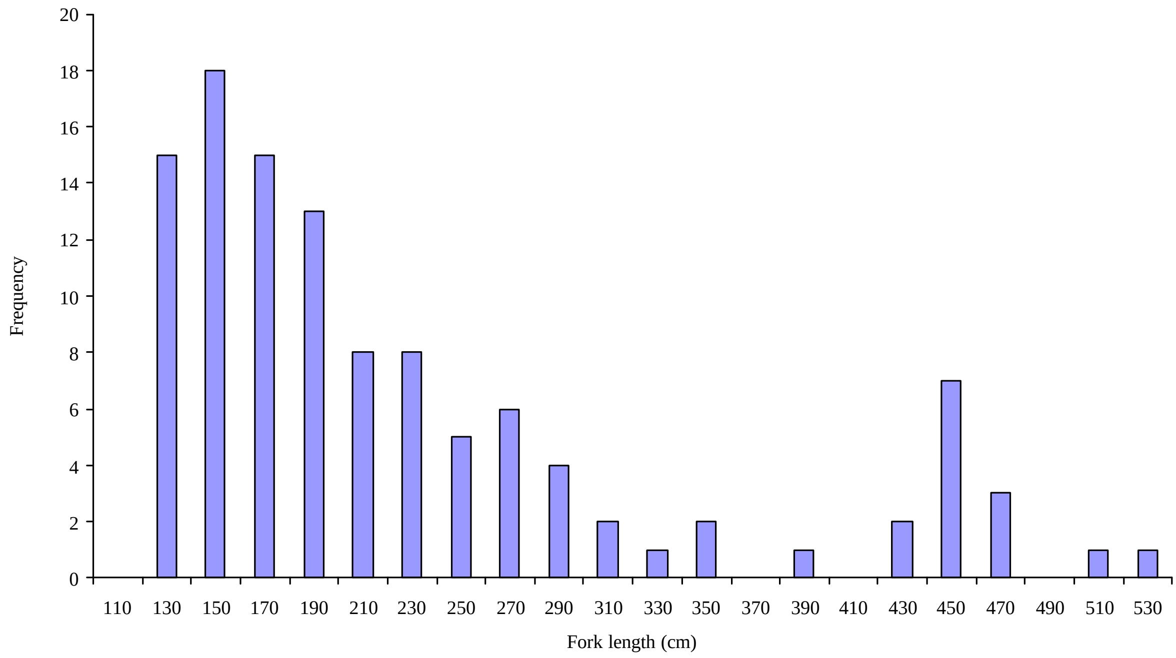

Figure 7. Length frequency histograms of the fork lengths of white sharks for which vertebrae are available. n=112.

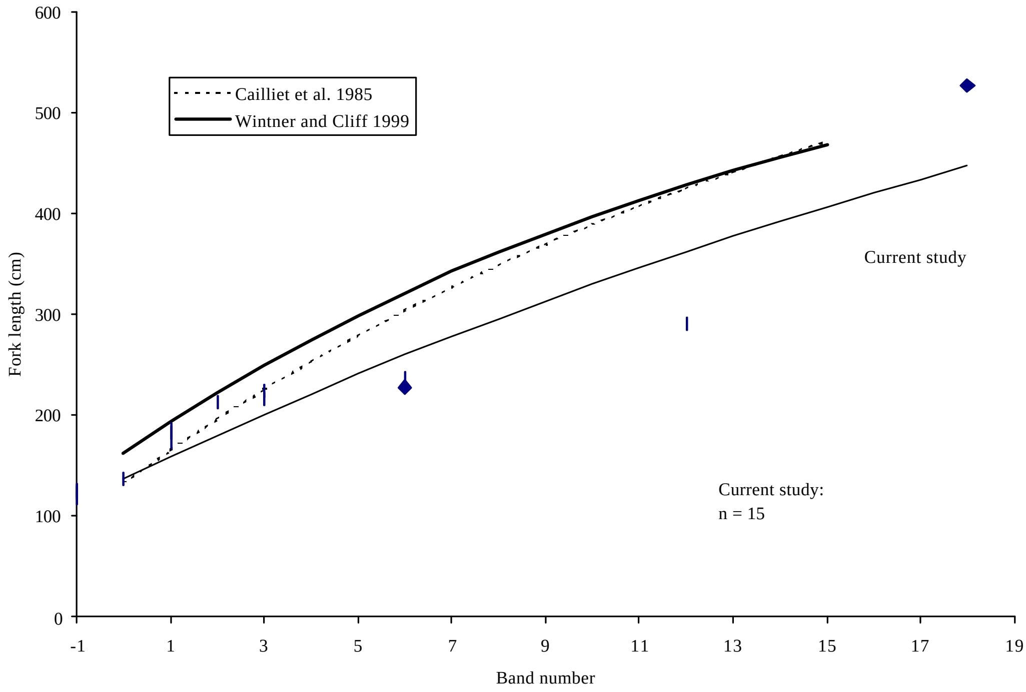

Figure 8. Comparison of white shark growth data. Solid diamonds are the vertebral band counts from this study, thin solid line is the von Bertalanffy growth curve associated with these counts. Dashed line is the von Bertalanffy growth curve from Cailliet et al. (1985). Solid thick line is the von Bertalanffy growth curve from Wintner et al. (1999).

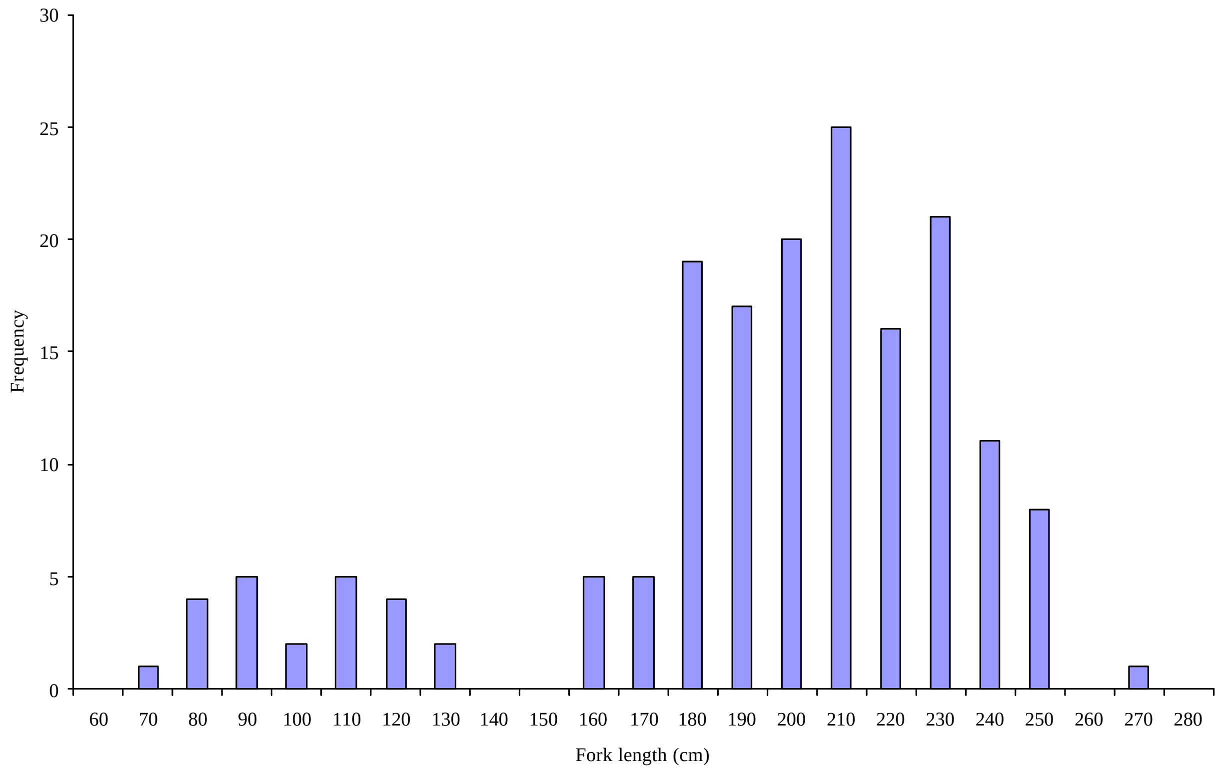

Figure 9. Length frequency histograms of the fork lengths of thresher sharks for which vertebrae are available. n=171.

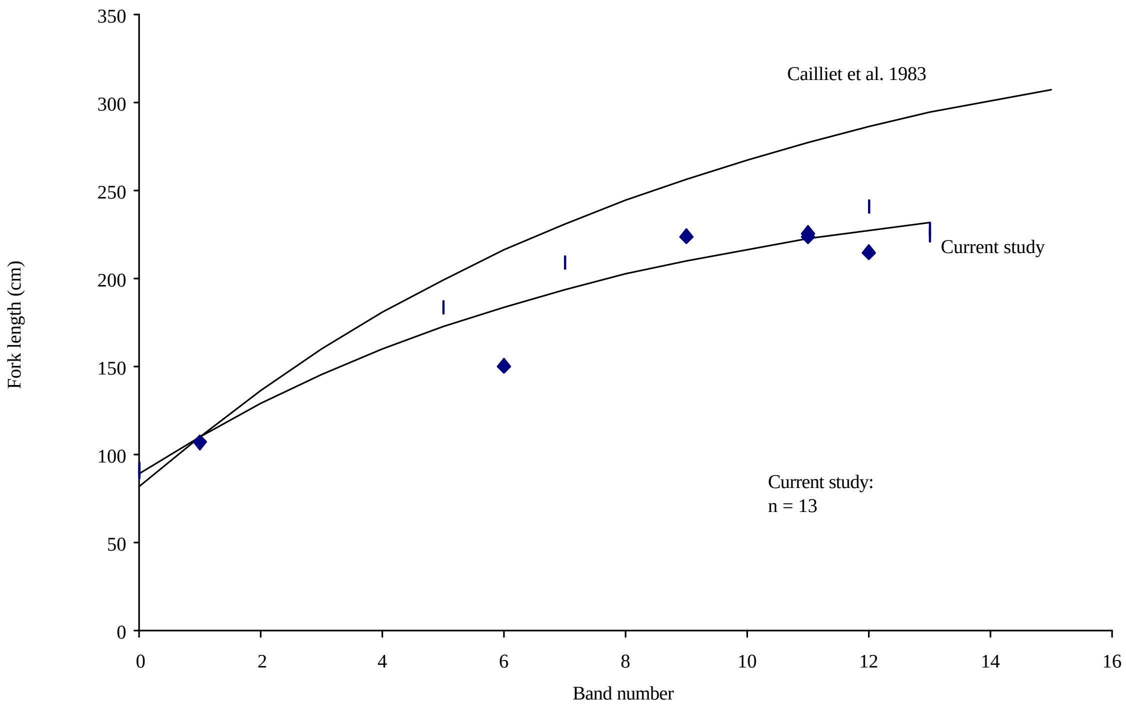

Figure 10. Comparison of thresher shark growth data. Solid diamonds are the vertebral band counts from this study, thin solid line is the von Bertalanffy growth curve associated with these counts. Solid thick line is the von Bertalanffy growth curve from Cailliet et al. (1983).